

**Absolute Brain Size Predicts Dog Breed Differences  
in Executive Function**

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## Abstract

Large-scale phylogenetic studies of animal cognition have revealed robust links between absolute brain volume and species differences in executive function. However, past comparative samples have been composed largely of primates, which are characterized by evolutionarily derived neural scaling rules. Therefore, it is currently unknown whether positive associations between brain volume and executive function reflect a broad-scale evolutionary phenomenon, or alternatively, a unique consequence of primate brain evolution. Domestic dogs provide a powerful opportunity for investigating this question due to their close genetic relatedness, but vast intraspecific variation. Using citizen science data on more than 7,000 purebred dogs from 74 breeds, and controlling for genetic relatedness between breeds, we identify strong relationships between estimated absolute brain weight and breed differences in cognition. Specifically, larger-brained breeds performed significantly better on measures of short-term memory and self-control. However, the relationships between estimated brain weight and other cognitive measures varied widely, supporting domain-specific accounts of cognitive evolution. Our results suggest that evolutionary increases in brain size are positively associated with taxonomic differences in executive function, even in the absence of primate-like neuroanatomy. These findings also suggest that variation between dog breeds may present a powerful model for investigating correlated changes in neuroanatomy and cognition among closely related taxa.

**Keywords:** cognitive evolution, brain evolution, brain size, executive function, breed differences, citizen science

## 1. Background

Comparative studies suggest that variance in brain size is linked to species differences in some aspects of cognition (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016; Deaner, Isler, Burkart, & Van Schaik, 2007; Garamszegi & Eens, 2004; Kotrschal et al., 2013; Kotrschal, Corral-Lopez, Amcoff, & Kolm, 2015; MacLean et al., 2014; Madden, 2001; Overington, Morand-Ferron, Boogert, & Lefebvre, 2009; Reader & Laland, 2002; Shultz & Dunbar, 2010; Sol, Bacher, Reader, & Lefebvre, 2008; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Studies of relative brain size have revealed interspecific links with problem solving in carnivores (Benson-Amram et al., 2016) and innovativeness in birds (Overington et al., 2009), while intraspecific examinations have linked relative brain size to numerical learning, spatial learning, and reversal learning in guppies (Buechel, Boussard, Kotrschal, van der Bijl, & Kolm, 2017; Kotrschal et al., 2013, 2015). Phylogenetic studies of absolute brain size have demonstrated a strong relationship between absolute brain volume and components of executive function (a suite of cognitive abilities involved in behavioral control, including working memory and inhibition) (Deaner et al., 2007; MacLean et al., 2014; Shultz & Dunbar, 2010). However, much of the work linking absolute brain size to executive function has been conducted with primates, and recent advances in comparative neuroanatomy reveal that primates are characterized by unique neural scaling properties, which contrast with those of other orders (Herculano-Houzel, 2012, 2017; Herculano-Houzel, Collins, Wong, & Kaas, 2007). Specifically, in most mammals, as brain volume increases, average neuron size tends to increase as well, and neurons become less densely populated in the brain (Herculano-Houzel, 2014, 2017; Herculano-Houzel, Mota, & Lent, 2006). In contrast, as primate brains increase in volume, both neuron size and density remain constant, resulting in isometric (i.e. 1:1) scaling between these variables (Herculano-Houzel et al.,

2007). As a result, for a given primate and non-primate mammal of equivalent brain size, the primate's brain is expected to contain more neurons and to have greater neuron density. Similarly, in primates, a two-fold change in brain volume is expected to lead to a two-fold increase in the number of neurons in the larger brain, whereas a two-fold change in volume leads to the addition of many fewer neurons in non-primate mammals. This phenomenon has been proposed to account for the uniqueness of the human brain (but see [Mortensen et al., 2014] for evidence that long-finned pilot whales have more neocortical neurons than humans, but lower neuron density), the 'primate advantage' of increases in brain volume, and previously observed associations between brain volume and species differences in executive function (Deaner et al., 2007; Herculano-Houzel, 2012; MacLean et al., 2014). Consequently, it remains unknown whether the relationship between brain volume and executive function reflects a broad-scale evolutionary phenomenon, or alternatively, a unique consequence of primate brain evolution.

Therefore, an important test of the association between brain volume and executive function requires analysis with a large sample of taxa that do not adhere to primate-like neural scaling rules. Domesticated dogs, with their extraordinary degree of intraspecific morphological variation (including variation in brain size [Kruska, 1988; Wosinski, Schleicher, & Zilles, 1996]), offer a unique opportunity for such a study. New evidence shows that dogs adhere to the same cortical scaling rules as other non-primate mammals, and that domestication appears to have had no effect on allometric brain scaling in dogs (or other domesticated carnivores examined) (Jardim-Messeder et al., 2017). Additionally, previous phylogenetic studies of links between brain size and cognition have been critiqued for ignoring heterogeneity resulting from variation in evolutionary trajectories or different selection pressures on neuroanatomy across taxa (Logan et al., 2018). As the relative sizes of different brain structures are likely to be less variable within, than across

species (Finlay & Darlington, 1995; Gould et al., 2013; Healy & Krebs, 1992; Lucas, Brodin, de Kort, & Clayton, 2004) dogs allow us to assess the cognitive correlates of changes in absolute brain size while better controlling for changes in the relative sizes of specific brain regions, or other factors that vary considerably across diverse taxonomic groups (Barton & Harvey, 2000; Barton & Venditti, 2014; Gould et al., 2013). Although breed-level variation in neuroanatomy remains largely unexplored, preliminary data suggest that the relative sizes of neural structures do not vary significantly across dog breeds with large degrees of variation in brain volume and skull shape (Roberts, McGreevy, & Valenzuela, 2010; Thames et al., 2009).

Here we report the results of analyses investigating the association between estimated brain weight and breed differences in dog cognition, measured in a sample of more than 7,000 individuals from 74 breeds, on a battery of cognitive tests designed to probe diverse aspects of cognition (broadly defined as the processes through which animals acquire, store, and act on information from the environment [Shettleworth, 2009]).

## **2. Methods**

Cognitive data were collected through *Dognition.com*, a citizen science website that provides dog owners with instructions for completing cognitive experiments with pet dogs in their homes (Bonney et al., 2009; Cooper, 2016). Analyses of these data replicate findings from similar tests conducted in laboratory settings (Stewart et al., 2015), and psychometric analyses of citizen science data yield underlying factors consistent with those obtained from conventional approaches (MacLean, Herrmann, Suchindran, & Hare, 2017). We included data from all ten of Dognition's primary cognitive tasks in our analyses, measuring a wide range of cognitive skills including components of executive function, inferential and causal reasoning, and communicative processes (Table 1, Online Resource 1). We analyzed data from 7,397 purebred adult dogs representing 74

94 breeds (Online Resource 1: Tables 1-3). Breed-average body weights were compiled from the  
95 Canine Behavioral Assessment and Research Questionnaire (C-BARQ) (Hsu & Serpell, 2003;  
96 McGreevy et al., 2013), and breed-average brain weights were estimated from a scaling function  
97 described by Bronson (1979) and validated using C-BARQ body weights for a sample of 24 breeds  
98 with known brain weights (Online Resource 1: Figure 1). To control for genetic relatedness  
99 between breeds, the associations between estimated brain weight and cognitive measures were  
100 tested using Efficient Mixed Modeling for Association studies (EMMA) (Kang et al., 2008; Zhou  
101 & Stephens, 2012). Genetic covariance between breeds was incorporated using a breed-average  
102 identity-by-state (IBS) matrix (Boyko et al., 2010), using molecular data from Hayward and  
103 colleagues (2016). For analyses including individual level data across breeds, breed-level IBS  
104 matrices were multiplied by an individual-level incidence matrix to generate an individual-level  
105 IBS matrix. To avoid the assumption that members of the same breed were clonal, pairwise within-  
106 breed IBS values were set to the average IBS value between members of that breed. Tests were  
107 conducted using the ‘EMMREML’ package (Akdemir & Godfrey, 2015) in the R environment  
108 (v.3.3.1) (R Core Team, 2016). Associations were considered significant at an alpha level of 0.05.  
109 Data are available as electronic supplementary material (Online Resource 2).

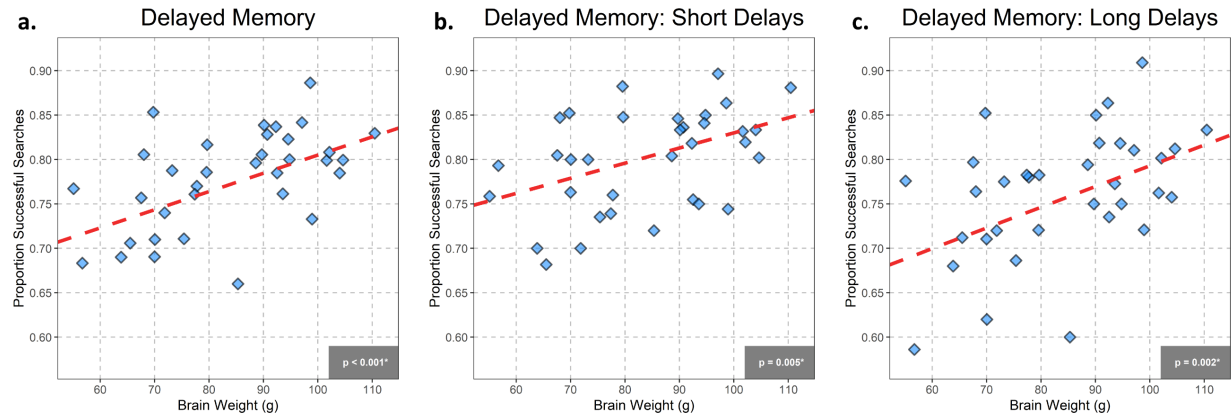
110 **Table 1**

Task	Description	Total dogs	Total breeds	$\beta$	$\chi^2$	p
Yawning	While sitting on the floor, the owner yawns audibly every 5 seconds for 30 seconds total. The dependent measure is the difference between whether or not the dog yawns during the 30 second trial and a control condition. Two trials are conducted.	7344	74	-0.00053	1.19	0.27
Eye Contact	The owner stands holding a treat directly below his or her eye and makes eye contact with the dog. The dependent measure is how long it takes the dog to break eye contact for longer than two seconds. Three trials are conducted.	6413	69	-0.018	0.12	0.73
Arm Pointing	The owner places two treats at arm's length on his or her right and left. The owner then points to one of these locations. The dependent measure is which location the dog approaches first as the owner sustains pointing. Six trials are conducted.	4342	59	0.00068	4.18	<b>0.041*</b>
Foot Pointing	Same as Arm Pointing, but rather than pointing, the owner extends his or her foot toward one of the locations. The dependent measure is which location the dog approaches first as the owner keeps his or her foot extended. Six trials are conducted.	4044	58	-0.00013	0.15	0.70
Cunning	The owner places a treat in front of the dog while verbally forbidding the dog from taking it. The dependent measure is the difference between the time it takes for the dog to take the treat while the owner is watching and while the owner is not watching. Six trials are conducted.	2710	44	-0.10	13.15	<b>&lt;0.001*</b>
Watching Condition		2711	44	0.33	9.98	<b>0.002*</b>
Not Watching Condition		2753	44	0.43	17.94	<b>&lt;0.001*</b>
Memory vs. Pointing	The owner places a treat under one of two cups in full view of the dog, and then points to the other cup. The dependent measure is which cup the dog approaches first as the owner sustains pointing. Six trials are conducted.	2123	36	-0.0013	3.99	<b>0.046*</b>
Memory vs. Smell	The owner places a treat under one of two cups in full view of the dog, and then blocks the dog's view while switching the treat to the other cup. The dependent measure is which cup the dog approaches first. Four trials are conducted.	1949	34	-0.00023	0.15	0.69
Delayed Memory	The owner places a treat under one of two cups in full view of the dog. The owner then waits 60, 90, 120, and 150 seconds across four trials before releasing the dog. The dependent measure is which cup the dog approaches first.	1888	34	0.0021	14.18	<b>&lt;0.001*</b>
Inferential Reasoning	The owner hides a treat under one of two cups and sham baits the other. The owner then lifts the incorrect cup to show that it is empty. The dependent measure is which cup the dog approaches first. Four trials are conducted.	1432	26	0.00011	0.03	0.87
Physical Reasoning	The owner places two sheets of folded paper flat on the ground, and hides a treat under one of them while the dog's view is blocked. The result is that the paper in the correct hiding location is propped up by the treat, while the other is not. The dependent measure is which hiding location the dog approaches first. Four trials are conducted.	1322	23	0.00042	0.30	0.59

111 **Table 1.** Descriptions of each cognitive task presented in the order in which they were conducted, the number of  
112 individual dogs contributing data per task, the number of breeds represented in each task's analysis, and results from  
113 mixed linear models (controlling for genetic relatedness) predicting cognitive performance from estimated brain weight  
114 for each task. Significant p-values are denoted in bold.

115

**Figure 1**



**Figure 1.** Scores on a measure of short-term memory (Delayed Memory) as a function of estimated absolute brain weight across dog breeds. The dashed lines shows the regression slopes from statistical models controlling for genetic relatedness between breeds **(a)** across all trials, **(b)** across short delays of 60 and 90 seconds, and **(c)** across long delays of 120 and 150 seconds. Each breed included in the analyses had at least 20 individuals complete this task, and is represented by one diamond.

### 3. Results

**(a) Absolute brain size predicts breed differences in executive function.** Based on previous studies linking absolute brain size to executive function, we hypothesized that larger-brained breeds would score higher on cognitive measures related to executive function. To test this hypothesis, we fit mixed-models predicting breed-average scores on two tasks indexing components of working memory (short-term memory) and of inhibitory control (self-control) as a function of estimated absolute brain weight. These models revealed significant associations between estimated brain weight and performance on both tasks (Table 1, Figure 1, Figure 2).

In the Delayed Memory task, larger-brained breeds correctly remembered the location of hidden food at significantly higher levels than smaller-brained breeds when examining performance after all delays lengths combined ( $\beta = 0.0021$ ,  $\chi^2(1) = 14.18$ ,  $p < 0.001$ ; Figure 1a), as well as after short (60s and 90s) and long (120s and 150s) delays (Short delays:  $\beta = 0.0017$ ,  $\chi^2(1) = 7.91$ ,  $p = 0.005$ , Figure 1b; Long delays:  $\beta = 0.0023$ ,  $\chi^2(1) = 9.70$ ,  $p = 0.001$ , Figure 1c).

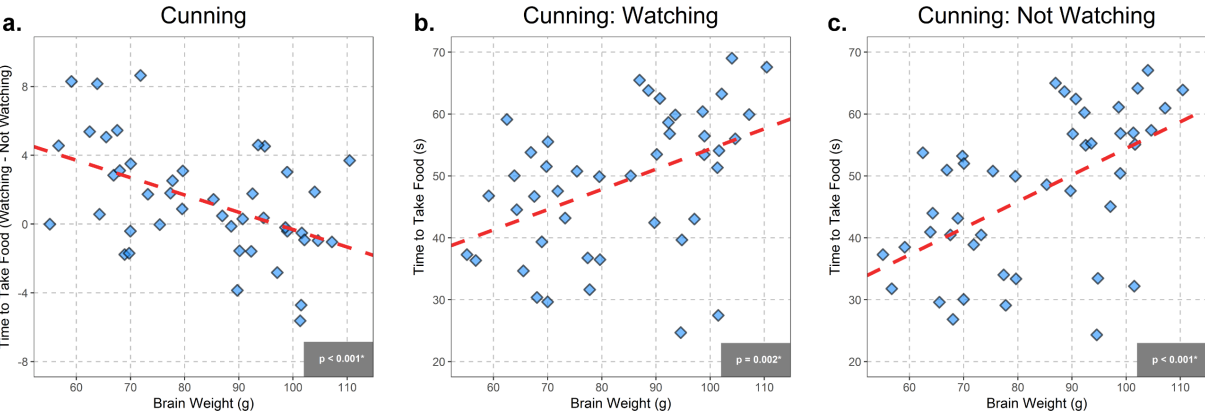


The slope of the association between estimated brain weight and performance was greater at long delays than short delays, suggesting that the gap in performance between breeds of varying brain size generally widens as a function of increased cognitive demands. The effect was weakest at 60 seconds ( $\beta = 0.0014$ ,  $\chi^2(1) = 2.84$ ,  $p = 0.09$ ), but became significant as delay length increased (90s:  $\beta = 0.0020$ ,  $\chi^2(1) = 6.99$ ,  $p = 0.01$ ; 120s:  $\beta = 0.0027$ ,  $\chi^2(1) = 5.78$ ,  $p = 0.02$ ; 150s:  $\beta = 0.0020$ ,  $\chi^2(1) = 5.18$ ,  $p = 0.02$ ).

In the Cunning task, dogs were prohibited from eating a visible food reward, and whether the experimenter watched the dog varied across conditions. Although designed as a measure of sensitivity to human perception, all conditions in this task pose demands on self-control, as dogs were required to inhibit a desire to consume the visible food (see Müller and colleagues [2016] for a similar measure assessing self-control in dogs). In this task, larger-brained breeds were significantly slower to pilfer prohibited food placed directly in front of them than smaller-brained breeds in a condition where a human's eyes were closed or back was turned (Not Watching), compared to a condition where a human actively watched the subject (Watching;  $\beta = -0.10$ ,  $\chi^2(1) = 13.15$ ,  $p < 0.001$ ; Figure 2). Although greater self-control is likely required to inhibit the desire to steal food when not being actively monitored, variation in perspective-taking ability may also contribute to this effect, or smaller-brained breeds may simply be more likely to restrain their actions while being monitored. Thus, we conducted separate analyses of the Watching and Not Watching conditions for this task. In both conditions, larger-brained breeds exhibited greater self-control by waiting significantly longer to eat the forbidden food ([Cunning] Watching:  $\beta = 0.33$ ,  $\chi^2(1) = 9.98$ ,  $p = 0.002$ ; [Cunning] Not Watching:  $\beta = 0.43$ ,  $\chi^2(1) = 17.94$ ,  $p < 0.001$ ). Additionally, the slope of the association between estimated brain weight and time to pilfer food was greater in the Not Watching condition than in the Watching condition, supporting the idea that greater self-

control is required to resist temptation when not being actively monitored. Therefore, with increased task difficulty in both the Cunnig and Delayed Memory tasks, the slopes of the associations between cognitive performance and brain size generally become more pronounced.

**Figure 2**



**Figure 2.** Difference scores between the Watching and Not Watching conditions in the Cunnig task (a) and scores on measures of self-control ([b] Cunning: Watching condition; [c] Cunning: Not Watching condition) as a function of estimated brain weight across dog breeds. The dashed lines show the regression slopes from statistical models controlling for genetic relatedness between breeds. Each breed included in the analyses had at least 20 individuals complete this task, and is represented by one diamond.

**(b) Associations between brain size and cognition vary across cognitive domains.** A

fundamental question in the cognitive sciences is whether skills for solving diverse problems are subserved by a common set of cognitive processes that are flexibly applied across contexts (domain generality), or alternatively, by specialized processes that are differentially applied in specific contexts (domain specificity). Due to the practical challenges of conducting cognitive experiments with large samples of species, most previous studies investigating links between brain volume and cognition used a small number of cognitive tasks, precluding assessment of the specificity of associations between brain size and measures of cognition. To test the predictions of the domain-general and domain-specific hypotheses, we investigated whether estimated brain

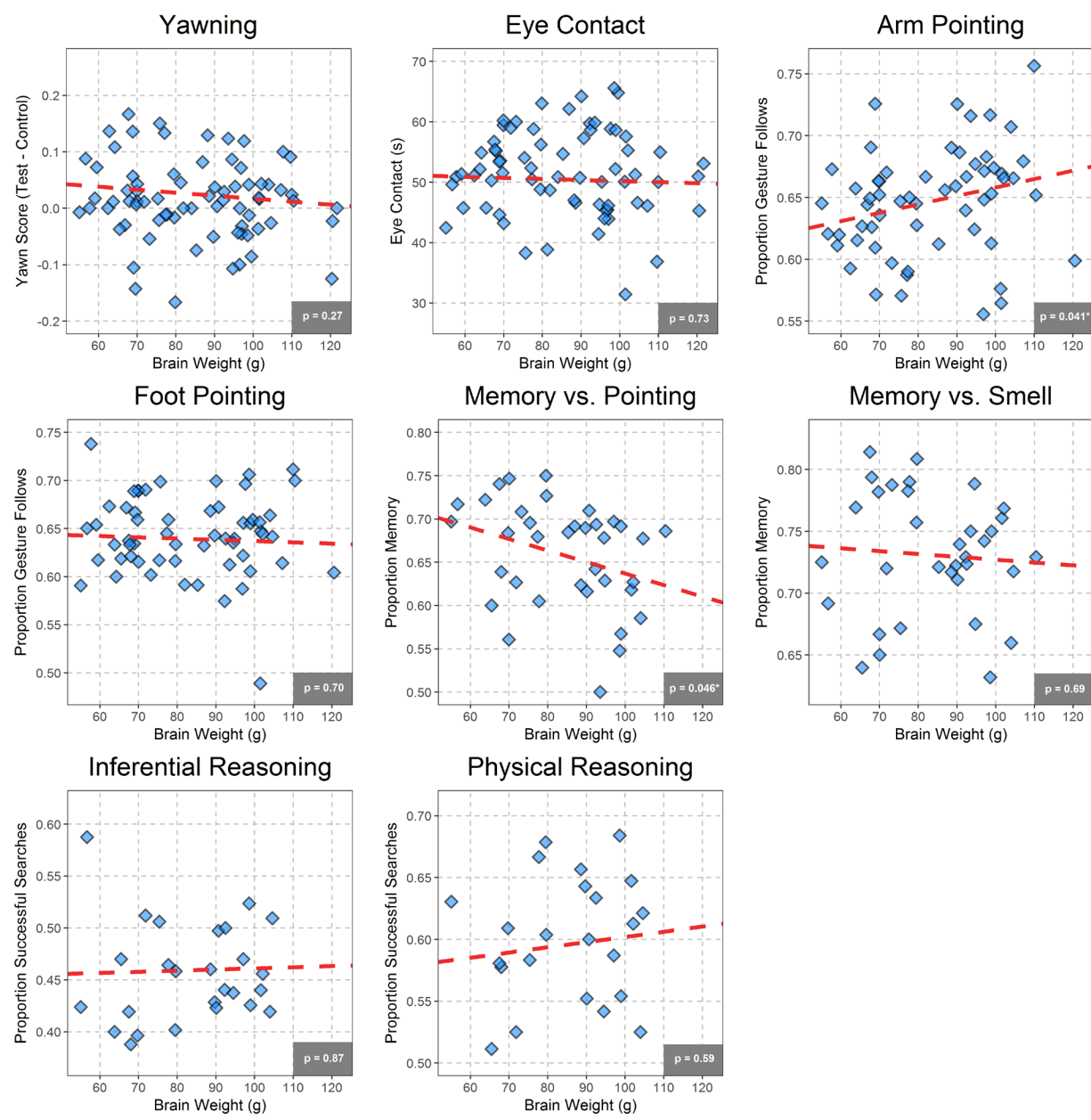
weight broadly predicts breed differences across diverse cognitive measures, or alternatively, if these associations are limited to executive function.

Consistent with domain-specific hypotheses (Amici, Barney, Johnson, Call, & Aureli, 2012; MacLean et al., 2017), the relationship between estimated brain weight and breed differences in cognition was highly variable across the ten cognitive measures (Table 1, Figure 3). For 6 of the 10 tasks, there was no association between estimated brain weight and breed-average performance ([contagious] Yawning:  $\beta = -0.00053$ ,  $\chi^2(1) = 1.19$ ,  $p = 0.27$ ; Eye Contact:  $\beta = -0.018$ ,  $\chi^2(1) = 0.12$ ,  $p = 0.73$ ; Foot Pointing:  $\beta = -0.00013$ ,  $\chi^2(1) = 0.15$ ,  $p = 0.70$ ; Memory vs. Smell:  $\beta = -0.00023$ ,  $\chi^2(1) = 0.15$ ,  $p = 0.69$ ; Inferential Reasoning:  $\beta = 0.00011$ ,  $\chi^2(1) = 0.03$ ,  $p = 0.87$ ; Physical Reasoning [visual causality]:  $\beta = 0.00042$ ,  $\chi^2(1) = 0.30$ ,  $p = 0.59$ ). In addition to significant associations between estimated brain weight and components of executive function, larger-brained breeds were also significantly more likely to search for food in a location indicated by an arm-pointing gesture (Arm Pointing:  $\beta = 0.00068$ ,  $\chi^2(1) = 4.18$ ,  $p = 0.041$ ), and were significantly more likely to rely on this pointing gesture when it was pitted against their own memory of where food had been hidden (Memory vs. Pointing:  $\beta = -0.0013$ ,  $\chi^2(1) = 3.99$ ,  $p = 0.046$ ).

To explore whether behavioral data were stable across trials within tasks significantly associated with estimated brain weight, and whether any variation across time differed as a function of estimated brain weight, we fit mixed-models predicting task performance from trial number alone, as well as from a trial number by estimated brain weight interaction term. To account for repeated measures, all models included a random intercept for breed. Trial number alone was significant predictor of task performance in Cunnig due to dogs pilfering forbidden food significantly faster over the course of the trials in the Watching condition but not in the Not

201 Watching condition, as well as in Memory vs. Pointing such that dogs became less likely to follow  
202 the pointing gesture over time (Online Resource 1). However, in no cases were there any  
203 significant trial number by estimated brain weight interactions (Online Resource 1). The lack of  
204 significant interactions between trial number and brain weight demonstrates that while  
205 performance varied across trials in some measures, it did not vary differentially across breeds as a  
206 function of brain weight. Therefore, the significant associations identified between estimated brain  
207 weight and cognitive performance in our main analyses are unlikely to be due to differential  
208 learning between small and large-brained breeds over the course of each task.

209 **Figure 3**



210  
211 **Figure 3.** Scores on all cognitive tasks except Delayed Memory and Cunning (see Figure 1 and Figure 2) as a function  
212 of estimated brain weight across dog breeds. The dashed lines show the regression slopes from statistical models  
213 controlling for genetic relatedness between breeds. Each breed included in the analyses had at least 20 individuals  
214 complete a given task, and is represented by one diamond.

**(c) Individual-level analyses.** To examine how within-breed variation in cognition may influence our results, we fit mixed-models predicting scores on each task as a function of breed-average estimated brain weight on an individual level (Online Resource 1: Table 4). Results from these individual-level analyses largely mirrored those from the main breed-level analyses: Estimated brain weight was again a significant predictor of performance in each measure which primarily indexed components of executive function (Delayed Memory:  $\beta = 0.0015$ ,  $\chi^2(1) = 11.06$ ,  $p < 0.001$ ; [Cunning] Watching:  $\beta = 0.27$ ,  $\chi^2(1) = 10.25$ ,  $p = 0.001$ ; [Cunning] Not Watching:  $\beta = 0.33$ ,  $\chi^2(1) = 15.34$ ,  $p < 0.001$ ), as well as difference scores between conditions in the Cunning task ( $\beta = -0.080$ ,  $\chi^2(1) = 13.40$ ,  $p < 0.001$ ) and performance in Arm Pointing ( $\beta = 0.00068$ ,  $\chi^2(1) = 6.51$ ,  $p = 0.01$ ). However, unlike results from the breed-level analyses, the association between estimated brain weight and performance in Memory vs. Pointing fell slightly above the significance threshold ( $\beta = -0.0011$ ,  $\chi^2(1) = 3.64$ ,  $p = 0.056$ ), while a significant association emerged between estimated brain weight and performance in Physical Reasoning ( $\beta = 0.00092$ ,  $\chi^2(1) = 4.00$ ,  $p = 0.045$ ).

**(d) Body size.** As breed-average brain weights were estimated from breed-average body weights in our main analyses, we expected to find many similar associations between cognition and body size. Mixed-models predicting task scores as a function of CBARQ-reported breed-average body weight generally revealed the same pattern of results as those using breed-average estimated brain weight as the predictor; body weight was a significant predictor of performance in Delayed Memory, Cunning, and the Watching and Not Watching conditions analyzed separately, but associations between body weight and Arm Pointing ( $p = 0.07$ ) and Memory vs. Pointing ( $p = 0.06$ ) fell slightly above the significance threshold (Online Resource 1). In the majority of cases, linear models using estimated brain weight as the predictor had a lower AIC and explained a larger proportion of the variance in cognitive measures as compared to models using body weight as the

predictor, but differences in AIC and adjusted  $R^2$  were generally small (Online Resource 1). Even in studies using more direct measures of brain size rather than estimation, the challenge of disentangling associations with absolute brain size and body size is evident as the two variables are often very highly correlated (MacLean et al., 2014).

To explore whether the same associations between cognition and brain size would emerge when estimating breed-average brain weight independently from body weight, we compiled breed-average skull measurements from Boyko et al. (2010) for a subset of breeds ( $n = 27$ ) for whom data was available. To assess which skull measures best predicted brain weight, we first fit a multiple regression model predicting known breed-average brain weights from Bronson (1979) using breeds for which both skull measurements and brain weights were available ( $n = 12$ ) as a function of cranial depth, maximum cranial width, and least cranial width. As results from this model showed that only cranial depth was a significant predictor of brain weight controlling for the other predictors, we next fit a simple linear regression model predicting brain weight from cranial depth alone. Breed-average cranial depth explained a greater proportion of the variance in brain weight and had a lower model AIC ( $\beta = 0.01$ ,  $F(1, 10) = 119.4$ ,  $p < 0.001$ , adjusted  $R^2 = 0.92$ , AIC = 82.13) than did CBARQ-reported breed-average body weight in this same subset ( $\beta = 1.03$ ,  $F(1, 10) = 62.83$ ,  $p < 0.001$ , adjusted  $R^2 = 0.85$ , AIC = 89.03), suggesting that cranial depth was a better predictor of brain weight than was body weight in this sample. We then used cranial depth to predict breed-average brain weight across the 27 breeds for which cognitive data and skull measurements were available. Lastly, we fit mixed-models (controlling for genetic relatedness between breeds) predicting scores on each cognitive task as a function these new brain weight estimates. Breed-average brain weight estimated from cranial depth significantly predicted performance in each measure which primarily indexed components of executive function (Delayed

Memory:  $\beta = 0.0014$ ,  $\chi^2(1) = 4.91$ ,  $p = 0.03$ ; [Cunning] Watching:  $\beta = 0.43$ ,  $\chi^2(1) = 4.51$ ,  $p = 0.03$ ; [Cunning] Not Watching:  $\beta = 0.49$ ,  $\chi^2(1) = 6.72$ ,  $p = 0.01$ ), but did not significantly predict performance in Arm Pointing ( $\beta = -0.0002$ ,  $\chi^2(1) = 0.09$ ,  $p = 0.76$ ), Memory vs. Pointing ( $\beta = 0.0002$ ,  $\chi^2(1) = 0.02$ ,  $p = 0.89$ ), or difference scores between conditions in the Cunning task ( $\beta = -0.06$ ,  $\chi^2(1) = 0.69$ ,  $p = 0.41$ ). Therefore, estimates of breed-average brain weight derived independently of breed-average body weight were significantly associated with measures of short-term memory and self-control, but not other cognitive measures.

The findings above reveal a range of associations between estimated brain weight and breed differences in cognition. However, it remains possible that additional factors, which covary with body weight and brain weight, may partially account for these associations. To address this possibility, we conducted additional analyses with potentially confounding variables.

**(e) Perceptual factors.** Previous studies suggest that skull shape is associated with aspects of visual perception in dogs. Specifically, brachycephalic dogs (defined by a high cephalic index (CI), see Online Resource 1) are characterized by more forward-facing eyes and greater ocular overlap (Gácsi, McGreevy, Kara, & Miklósi, 2009; Helton & Helton, 2010). Gácsi et al. (2009) found that brachycephalic breeds were significantly better at following human pointing cues as compared to dolichocephalic breeds (low CI), and suggested that this result may be partially attributable to breed differences in visual perception. Our sample contained 50 breeds for which CI measurements were reported in (McGreevy et al., 2013) or (Boyko et al., 2010), and in these breeds, CI was significantly negatively correlated with estimated brain weight ( $r = -0.43$ ,  $p = 0.002$ ). Thus, explanations invoking breed differences in vision yield predictions opposite to what we observed in measures of short-term memory, self-control, and gesture following. Indeed, in breeds for which both cognitive and CI data were available, CI was significantly negatively



correlated with performance in measures of short-term memory and self-control (Delayed Memory:  $r = -0.47$ ,  $p = 0.02$ ; [Cunning] Watching:  $r = -0.41$ ,  $p = 0.02$ ; [Cunning] Not Watching:  $r = -0.52$ ,  $p = 0.002$ ), and was not significantly correlated with measures of gesture following (Arm Pointing:  $r = -0.19$ ,  $p = 0.24$ ; Memory vs. Pointing:  $r = -0.04$ ,  $p = 0.85$ ). Additionally, because we do not find consistent relationships between estimated brain weight and cognitive performance across tasks incorporating highly similar experimental set-ups and identical stimulus presentation distances, it is highly unlikely that breed differences in vision play a large role in the relationships we observed.

**(f) Training history.** A second important consideration relates to possible effects of training history on these cognitive measures. Using questionnaire data submitted to *Dognition.com*, we found that breeds with larger brains were more likely to have attended at least one obedience class ( $r = 0.71$ ,  $p < 0.001$ ), and were more likely to have been extensively trained ( $r = 0.75$ ,  $p = 0.01$ ). Although this information was not available for the majority of our subjects (precluding inclusion as a covariate in the main breed-level analyses), we fit mixed-models predicting scores on each task as a function of breed-average estimated brain weight and owner-reported extent of training history on an individual level including dogs for which both measures were available (Table 2). These analyses revealed that controlling for training history, estimated brain weight was a significant predictor of performance in each measure which primarily indexed components of executive function (Delayed Memory:  $\beta = 0.0015$ ,  $\chi^2(1) = 4.22$ ,  $p = 0.04$ ; [Cunning] Watching:  $\beta = 0.35$ ,  $\chi^2(1) = 12.95$ ,  $p < 0.001$ ; [Cunning] Not Watching:  $\beta = 0.38$ ,  $\chi^2(1) = 17.93$ ,  $p < 0.001$ ), but was not a significant predictor of performance in any other measures (Yawning:  $\beta = -0.00043$ ,  $\chi^2(1) = 0.21$ ,  $p = 0.64$ ; Eye Contact:  $\beta = -0.068$ ,  $\chi^2(1) = 1.17$ ,  $p = 0.28$ ; Arm Pointing:  $\beta = 0.00056$ ,  $\chi^2(1) = 1.78$ ,  $p = 0.18$ ; Foot Pointing:  $\beta = -0.00020$ ,  $\chi^2(1) = 0.17$ ,  $p = 0.68$ ; Cunning:  $\beta = -0.028$ ,

307  $\chi^2(1) = 0.25$ ,  $p = 0.62$ ; Memory vs. Pointing:  $\beta = -0.00095$ ,  $\chi^2(1) = 0.91$ ,  $p = 0.34$ ; Memory vs.  
 308 Smell:  $\beta = -0.00021$ ,  $\chi^2(1) = 0.078$ ,  $p = 0.78$ ; Inferential Reasoning:  $\beta = 0.00082$ ,  $\chi^2(1) = 1.17$ ,  $p =$   
 309  $0.28$ ; Physical Reasoning:  $\beta = 0.0011$ ,  $\chi^2(1) = 2.42$ ,  $p = 0.12$ ). Therefore, as in the breed-level  
 310 analyses, estimated brain weight was a significant predictor of performance on measures of short-  
 311 term memory and self-control, even after controlling for training history on an individual level.  
 312 However, unlike results from the main breed-level analyses (but mirroring the pattern of results  
 313 obtained using cranial depth rather than body weight to estimate brain weight in a subset of our  
 314 sample), estimated brain weight was not a significant predictor of difference scores between  
 315 conditions in the Cunning task or of reliance on gesture following in Arm Pointing or Memory vs.  
 316 Pointing after controlling for training history. We also found that controlling for estimated brain  
 317 weight, training history was a significant predictor of performance in the Watching ( $\beta = 8.67$ ,  $\chi^2(1)$   
 318  $= 31.08$ ,  $p < 0.001$ ) and Not Watching ( $\beta = 8.55$ ,  $\chi^2(1) = 30.02$ ,  $p < 0.001$ ) conditions of the  
 319 Cunning task, as well as in Eye Contact ( $\beta = 3.60$ ,  $\chi^2(1) = 15.87$ ,  $p < 0.001$ ), Arm Pointing ( $\beta =$   
 320  $0.024$ ,  $\chi^2(1) = 8.18$ ,  $p = 0.004$ ), Memory vs. Pointing ( $\beta = -0.041$ ,  $\chi^2(1) = 5.94$ ,  $p = 0.015$ ), and  
 321 Inferential Reasoning ( $\beta = 0.029$ ,  $\chi^2(1) = 3.96$ ,  $p = 0.047$ ), but was not a significant predictor of  
 322 performance in the six remaining measures (Yawning:  $\beta = -0.018$ ,  $\chi^2(1) = 0.95$ ,  $p = 0.33$ ; Foot  
 323 Pointing:  $\beta = 0.0097$ ,  $\chi^2(1) = 1.11$ ,  $p = 0.29$ ; Cunning:  $\beta = 0.35$ ,  $\chi^2(1) = 0.16$ ,  $p = 0.69$ ; Memory vs.  
 324 Smell:  $\beta = -0.027$ ,  $\chi^2(1) = 3.55$ ,  $p = 0.059$ ; Delayed Memory:  $\beta = 0.026$ ,  $\chi^2(1) = 3.46$ ,  $p = 0.063$ ;  
 325 Physical Reasoning:  $\beta = 0.18$ ,  $\chi^2(1) = 1.71$ ,  $p = 0.19$ ). It is important to note that in measures of  
 326 self-control (Watching and Not Watching conditions of Cunning), both estimated brain weight and  
 327 training history made independent significant contributions to task performance, the latter of which  
 328 is unsurprising given that owners verbally forbid subjects from taking visible food (a commonly  
 329 trained command) as a part of the task.

330 **Table 2**

Task	n	Estimated Brain Weight			Training History		
		$\beta$	$\chi^2$	p	$\beta$	$\chi^2$	p
Yawning	1567	-0.00043	0.21	0.64	-0.018	0.95	0.33
Eye Contact	1452	-0.068	1.17	0.28	3.60	15.87	<b>&lt;0.001*</b>
Arm Pointing	1145	0.00056	1.78	0.18	0.024	8.18	<b>0.004*</b>
Foot Pointing	1102	-0.00020	0.17	0.68	0.0097	1.11	0.29
Cunning	905	-0.028	0.25	0.62	0.35	0.16	0.69
Watching Condition	905	0.35	12.95	<b>&lt;0.001*</b>	8.67	31.08	<b>&lt;0.001*</b>
Not Watching Condition	917	0.38	17.93	<b>&lt;0.001*</b>	8.55	30.02	<b>&lt;0.001*</b>
Memory vs. Pointing	793	-0.00095	0.91	0.34	-0.041	5.94	<b>0.015*</b>
Memory vs. Smell	749	-0.00021	0.078	0.78	-0.027	3.55	0.059
Delayed Memory	726	0.0015	4.22	<b>0.04*</b>	0.026	3.46	0.063
Inferential Reasoning	632	0.00082	1.17	0.28	0.029	3.96	<b>0.047*</b>
Physical Reasoning	608	0.0011	2.42	0.12	0.18	1.71	0.19

331 **Table 2.** Results from mixed linear models (controlling for breed-level genetic relatedness) predicting cognitive  
332 performance from breed-average estimated brain weight and owner-reported training history for each task on an  
333 individual level. The training history variable was derived from a questionnaire item asking owners, “How much  
334 training has your dog received?” Owners responded on an ordinal scale including “None,” “Little,” “Some,” and  
335 “Substantial” as response options. Significant p-values are denoted in bold.

336 **(g) Functional breed group classification.** A third consideration is that modern dog breeds have  
337 been selected for a variety of functional roles, with some roles (e.g. hunting and herding) requiring  
338 extensive cooperation with humans (Coppinger & Schneider, 1995). Previous studies suggest that  
339 dogs bred for cooperative roles may be more likely to follow human gestures (Udell, Ewald, Dorey,  
340 & Wynne, 2014; Wobber, Hare, Koler-Matznick, Wrangham, & Tomasello, 2009). Thus, to  
341 control for potential effects of breed group, we fit models including American Kennel Club (AKC)  
342 breed group designation and estimated absolute brain weight as predictors of performance. For the  
343 Memory vs. Pointing task, but none of the other measures significantly associated with estimated  
344 brain weight in the main analyses, a log likelihood ratio test revealed that controlling for brain  
345 weight, breed group was a significant predictor of performance ( $\chi^2(6) = 1.35$ ,  $p = 0.03$ ) but not  
346 vice-versa ( $\chi^2(1) = 0.04$ ,  $p = 0.15$ ). AKC-classified “Sporting” and “Working” breeds were the  
347 most likely to follow an arm-pointing gesture in this task (Sporting: mean = 0.60, SEM = 0.02;

Working: mean = 0.63, SEM = 0.02), while breeds in the “Terrier” and “Herding” groups were the least likely (Terrier: mean = 0.70, SEM = 0.01; Herding: mean = 0.69, SEM = 0.01). While increased tendencies to follow an arm-pointing gesture over memory in the Memory vs. Pointing task may be better explained by differences in AKC breed group than by differences in brain size, we find only mixed support for the idea that selection for cooperative roles is primarily responsible for this result, as breeds belonging to the Herding group were among the least likely to follow gestures in this task.

#### **4. Discussion**

Our findings support the hypothesis that increases in absolute brain size are associated with aspects of executive function, even in the absence of primate-like neuroanatomy. This result raises new questions about the cognitive consequences of evolutionary changes in brain size, and suggests that even within a species, brain size is associated with some aspects of cognition. By investigating intraspecific variance in a species characterized by high levels of morphological diversity, this study circumvents some challenges inherent to previous interspecific comparisons. Specifically, across species, differences in absolute brain volume can be confounded with changes in the relative proportions of specific brain regions. This phenomenon can arise both due to specialization of specific brain structures (mosaic brain evolution [Barton & Harvey, 2000; Barton & Venditti, 2014; Gould et al., 2013]) resulting from heterogeneity in selection pressures on neuroanatomical variation across taxa (Logan et al., 2018), or due to conserved developmental processes involving the timing of neurogenesis, which yield disproportionate enlargement of late developing structures (e.g. the neocortex) in larger-brained taxa (Finlay & Darlington, 1995; Kaas, 2000). Regarding the latter possibility, there are currently few data on the development of brain structures in dogs, but preliminary data suggest that breed differences in brain volume are less

subject to these conserved developmental constraints which induce allometry (deviation from 1:1 scaling) between total brain volume and specific regions of the brain. Specifically, in contrast to comparative mammalian samples, imaging studies have shown that there are no significant differences in the proportional sizes of the cerebellum, forebrain, or brainstem across dog breeds with widely varying total brain volumes (Thames et al., 2009), or in absolute size of the olfactory lobe across breeds with widely varying skull shapes (Roberts et al., 2010). This finding is consistent with the notion that allometric relationships which apply across species often do not hold within species (Armstrong, 1990), leading researchers to suggest that the extraordinary morphological variation of dogs makes this species an ideal candidate for investigating intraspecific brain scaling and the cognitive implications thereof (Jardim-Messeder et al., 2017).

Importantly, even with a lack of isometric (i.e. 1:1) scaling between brain volume and the number of neurons in the brain, larger dog brains are still expected to contain more neurons than smaller dog brains. In the only comparison of dog neuron counts to date, Jardim-Messeder and colleagues found that the cortex of a golden retriever with a body weight of 32kg contained 627 million neurons, while the cortex of an unknown breed with a body weight of 7.45kg contained 429 million neurons (Jardim-Messeder et al., 2017). Thus, if the number of neurons in the brain is expected to predict taxonomic differences in executive function (Herculano-Houzel, 2017), our findings are consistent with this hypothesis. However, because increases in volume are expected to result in the addition of many fewer neurons in dog brains than primate brains, we would theoretically expect differences in the slope of the relationship between brain volume and measures of executive function between these taxonomic groups given adequate control of extraneous variables.

A second major finding from this study is that the relationship between estimated brain weight and breed differences in cognition varied widely across cognitive tasks. For example, we found only limited evidence for an association between estimated brain weight and reasoning about causal properties of the world, and no evidence for an association between estimated brain weight and inferential reasoning, use of a novel communicative gesture (foot pointing), or measures of eye contact with a human. After controlling for training history at an individual level, we also found no evidence for an association between estimated brain weight and reliance on following communicative pointing cues to locate food. This result supports domain-specific accounts of cognition, and is consistent with previous comparative studies which have revealed links between brain volume and executive function, but no association between brain volume and other domains of cognition (MacLean et al., 2013). As suggested by domain specificity, absolute brain size is therefore unlikely to be an informative predictor of all cognitive abilities. However, absolute brain size may be particularly important for executive function, because these processes exert high-level ‘supervisory’ control over a variety of more specialized cognitive functions. Additionally, these results suggest that the significant associations between estimated brain weight and measures of executive function are unlikely to be artifacts of breed differences in motivation or perception, in which case we would have expected similar associations for all tasks involving a search for food, or requiring attention to visual stimuli in the frontal field.

One limitation of this study stems from the lack of individual-level brain weight data from the dogs in our sample. While the scaling function used to estimate breed-average brain weights described by Bronson (1979) explained an overwhelming proportion of the variance in brain weight (93%) in Bronson’s sample (26 breeds ranging from 3.6kg to 55.0kg in body weight), and a comparable percentage (91%) when using C-BARQ breed-average body weight as a predictor,

we cannot rule out the possibility that brain-to-body size scaling in breeds absent from Bronson's sample deviate from the scaling relationship used in our estimates. However, while estimates of brain weight based on body weight are subject to prediction error, the effects of this error are minimized in comparisons of taxa characterized by large differences in body size. Given the over 17-fold variation in body weight across breeds in our sample (range: 3.35kg – 59.75kg), and confirmation of a strong link between body and brain weight in dogs (Bronson, 1979), it is highly unlikely that prediction error substantially influenced our results. As expected given the strong association between body and brain weight, the observed associations between cognition and estimated absolute brain size were generally the same as those that exist between cognition and body weight in our sample. However, we found the same links between absolute brain size and executive function in a subset of our sample using brain weight estimated from skull measurements, rather than body weight. Relatedly, the exact intraspecific neural scaling rules of dog brains remain unknown, but it is of note that the two individuals examined in (Jardim-Messeder et al., 2017) fit the interspecific neural scaling rules that apply across non-primate mammals. Future work can address these limitations by examining how differences in cognition relate to variation in brain size and neuron count on an individual level both within and across dog breeds. Similarly, without independent measures of brain and body mass, we were unable to explore possible associations between relative brain size and performance on the cognitive tasks.

In conclusion, our findings suggest that evolutionary relationships between executive function and absolute brain size do not require primate-like neural scaling rules, that these relationships may be independent of changes in the relative sizes of specific areas of the brain, and that associations between brain size and cognition vary across cognitive domains. These findings raise new questions about how evolutionary shifts in brain size influence cognition across taxa,

439 and suggest that dog breeds provide a powerful and highly tractable model for assessing the  
440 cognitive consequences of neuroanatomical variation among close genetic relatives.



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## Competing Interests

BH is a founder of *Dognition.com* and a member of its Scientific Advisory Board. JC, JK, and ÁM are also members of the *Dognition.com* Scientific Advisory Board.

## Author Contributions

BH, JC, JK, ÁM, and ELM conceived and designed the experiments. DJH and ELM analyzed the data. DJH, BH, JC, JK, ÁM, and ELM wrote the paper.

## Data Accessibility

Data are available as electronic supplementary material.

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## Compliance with Ethical Standards

All animals included in this study were pet dogs tested by citizen scientists in their own homes. The use of third party data from *Dognition.com* was approved by Duke University

463 IACUC protocol A138-11-06 and data were collected in accordance with relevant guidelines and  
464 regulations.

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